

The General Biology of *Balanus glandula* Darwin

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THE CIRRIPEDE, *Balanus glandula* Darwin, is a common intertidal barnacle on the Pacific coast of North America, ranging from the Aleutian Islands to the northern border of Mexico. It appears to occupy much the same niche as that of *B. balanoides* (L.) on the eastern side of North America and the coasts of Europe. There has been much work recently on the latter species and it seemed of great interest to compare the general biology and ecology of the two species. A preliminary study is here reported; it has been made possible by the courtesy of Dr. D. B. Quayle of the Provincial Shellfish Laboratory, Ladysmith, Vancouver Island, Canada, and Dr. R. J. Menzies (and later, Dr. K. M. Budge) of the Scripps Institution of Oceanography, La Jolla, California. We wish to thank them for sending regularly samples of preserved material at about monthly intervals over a period of some 18 months.

THE GENERAL DISTRIBUTION

B. glandula has been found in the intertidal zone from the Aleutian Islands (52°N. Lat.) to the northern border of Mexico (32°25'N. Lat.) (Darwin, 1854; Pilsbry, 1916). Such an extensive distribution has been confirmed by Cornwall (1925, 1951, and 1955*b*). Ricketts and Calvin (1939) state that it is found at Ensenada (32°N. Lat.) and, although they admit that it may occur farther south, this appears to be about the southern limit, for Henry (1941) failed to find it in parts of Lower California and Mexico. Living under widely varying conditions of environment,

this cirripepe is found on wave-swept cliffs (35 miles south of the Mexican border) where all around *Chthamalus* sp. has become the dominant species on the open outer coast and in the quiet bays of enclosed water such as Puget Sound; it may thrive under conditions of poor circulation, low salinity, and slight wave action. At Pacific Grove, while absent from regions of excessively high surf on the open coast (the suggestion has even been made that this is due to the inability of the cyprids to settle under these conditions) it occurs at the uppermost levels of the shore. In more protected areas *B. glandula* is found at a level somewhat below high tide. It is often associated with *Acmaea digitalis* Eschscholtz (= *A. persona*) and *Littorina planaxis* (Nuttall). Although usually occupying a higher level than *Balanus cariosus* (Pallas), when the two are intermingled *B. glandula* may often be found attached to the former rather than to bare rock.

In the Puget Sound area the species appears to thrive best in places which differ markedly from those where it is found on the open coast (Shelford, 1930; Towler, 1930; Worley, 1930; Rice, 1930; Henry, 1940). According to these authors the barnacle is rarely crowded in this region, only a small number of elongated individuals being found; it is most abundant in the salinity range 26–30 parts per thousand and in a zone some three metres above low tide level. Worley (1930) has suggested that temperature is important in regulating the local distribution since the entrance of freshwater into Puget Sound during the summer not only reduces the salinity but also increases the temperature. Conse-

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quently, regions of lower salinity have a higher sea temperature (see also Rice, 1930). In the summer months the surface sea temperature in open water and where wave action is heavy ranges from 9–11°C., whereas in enclosed bays and areas protected from wave action it may reach 11–20°C. during the same period (Shelford and Towler, 1925). The greater temperature during the summer months in enclosed bays may also be responsible for the restriction of *B. glandula*, in such places, to the lower levels of the shore. *B. cariosus* is less resistant to reduced salinity, high temperatures, and products of decomposition than *B. glandula*, so that the latter penetrates farther into the brackish water.

B. glandula appears to have a variety of forms depending on its environment, and Pilsbry (1916) takes San Diego as a typical locality and discusses the variety of shapes which occur; conic or convexly conic with small aperture, at San Diego; more cylindrical, much less ribbed (some not at all) and with larger aperture, at San Francisco; a mixture of strongly ribbed, typical individuals and weakly ribbed, cylindrical ones with large aperture in the Puget Sound region. He describes shorter, obliquely conic forms on elongated, columnar individuals from Union Bay, Baynes Sound, British Columbia, and from Sitka both ribbed conic and smooth short, cylindrical forms; his Unalaska specimens were strongly ribbed with wider radii than the California type. Specimens from Atka, although similar to those from Unalaska in the walls, differed from all other types in their opercular valves. Barnacles are extremely plastic as regards their growth form, varying widely according to the conditions of the environment (Barnes and Powell, 1950) and without further work it may be doubted whether these varieties are subspecies or even local races; this has been confirmed by Henry (1942). The individuals used for this present work were similar to those of Pilsbry's typical locality; many examples of the "varieties" were, however, encountered.

Cornwall (1955a) refers to *B. glandula* as small, 10–18 mm. in diameter in uncrowded specimens and height a little more than half the diameter, and suggests that its extremely variable appearance is perhaps due to its wide range of habitat.

In contrast to some other common barnacles of the western coast of America, for example *B. cariosus* and *Chthamalus dalli* Pilsbry, *B. glandula* does not appear to be present in Japanese waters (Hiro, 1935).

MATERIAL AND METHODS

The collections were made at about monthly intervals from the shore at Ladysmith, Vancouver Island, and from the pier of the Scripps Institution of Oceanography at La Jolla.

At Ladysmith two series of samples were taken: one, for the examination of the gonads, from the intertidal zone between the 2 and 6 foot levels, was preserved in formalin and a second, which was preserved dry and used for size measurements, from the 5 foot level. At Ladysmith lower high water is + 9 feet and higher high water is 11–13 feet with a tidal range of some 16 feet. The samples from La Jolla were taken from the south side of the pier of Scripps Institution at a point where *B. glandula* forms a zone about 0.4 metre wide. The height of low water is 0.9 feet and the mean tidal range is 3.6 feet (Anon, 1953).

The state of the gonads was examined on about 50 individuals from each sample, the stage of development and colour of the ovaries or egg masses being noted as well as the condition of the male organs. The carino-rostral diameter of up to 150 animals was measured in each sample and an attempt made to separate the year classes by plotting cumulative percentages on arithmetic probability paper. When a new spat fall was well defined and could be clearly followed through several samples it was measured separately. The smaller animals were measured under a binocular microscope with a scaled ocular; for the larger animals calipers were used.

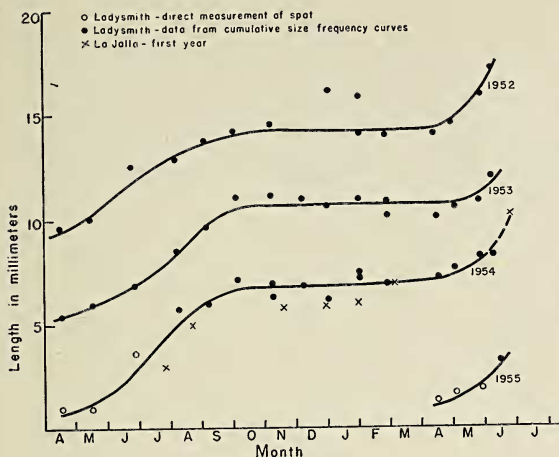


FIG. 1. Growth rate of *Balanus glandula* at Ladysmith, Vancouver Island, and at La Jolla, California.

GROWTH RATE

The cumulative frequency curves showed the presence of several distinct populations in each collection and, although the spread of any year group was considerable, the first three year groups could be separated with reasonable certainty (the subsidiary broods make little impression on the main populations). It is evident that growth takes place largely during the spring and summer months with relatively little or no growth in the winter. This is true both at Ladysmith and La Jolla, although at the latter there is some indication of growth during the winter months particularly of the first season. On the Ladysmith samples it was quite possible to follow directly from the spat fall the first season's growth; from a mean size of 1.2 mm. in April, a size of 7.0 mm. was reached by the end of the summer. At the end of the second season the mean size was some 11.0 mm. and it became 16.0 mm. at the end of the third season. Beyond this point deformities and crowding make the measurement less certain but it would seem that individuals reach a size of about 21 mm.

An examination of Figure 1 suggests that the growth rate at La Jolla is somewhat

slower than at Ladysmith; the mean size of the first year group tends to fall below that value for Ladysmith. Too much significance should not be attached to this possibility since marked individuals were not measured.

On one occasion a sample was available from Ladysmith that had been maintained at a very low tidal level. The growth rate was double that of the animals from the higher regions of the tidal zone, doubtless as a result of the greater periods of immersion at the lower levels (see Barnes and Powell, 1953).

BREEDING

The conditions of the ovaries or egg masses throughout the year are shown in Tables 1 (Ladysmith) and 3 (La Jolla) which give percentage of individuals at any particular stage of development.

At Ladysmith all the animals contained well-developed unfertilised creamy-yellow ovaries in the midwinter sample of December 8. At the same time the vesiculæ seminales were very prominent and the penes long and turgid. By January 3 some 20 per cent contained fertilised eggs present as firm light-yellow masses in the mantle cavity. On February 1 all individuals contained fertilised eggs, with 60 per cent in possession of eyed nauplii. It is clear that fertilisation probably begins in December and extends into January perhaps being a little less synchronous throughout the population than in some other species (Barnes and Barnes, 1954; Crisp, 1954; and Barnes, in press). As the embryos developed, the gorged appearance of the male organs disappeared, the seminal vesicles shrinking and becoming relatively inconspicuous; the penis became less turgid but there was no sign of gross regression.

By the end of February virtually the whole population contained eyed nauplii and these had been almost completely discharged by mid-April. Release into the plankton of the major brood takes place, therefore, in March. This gives a period of probably 2 months as the nearest estimate that can be made for the

TABLE 1

CONDITION OF THE OVARIES OF SPECIMENS OF *Balanus glandula* TAKEN AT LADYSMITH THROUGHOUT THE YEAR

DATE	PERCENTAGE OF SPECIMENS			
	Eggs unfertilised, not well defined	Eggs unfertilised, well defined, creamy yellow	Eggs fertilised, yellow	Eyed nauplii present, yellowish brown to brown
15/ 4/54.....	51	11	27	11
15/ 5/54.....	42	43		15
2/ 6/54.....	50	50		
30/ 6/54.....	← 100 →			
10/ 8/54.....	26	68	4	2
7/ 9/54.....	15	75	5	5
6/10/54.....	← 100 →			
10/11/54.....	20	80		
8/12/54.....		100		
3/ 1/55.....		80	20	
1/ 2/55.....			40	60
27/ 2/55.....			4	96
15/ 4/55.....	71	22		7
5/ 5/55.....	30	55	10	5
7/ 6/55.....	50	50		

period of incubation in the mantle cavity. However, some liberation of nauplii must take place later since eyed nauplii were found up to late May, but this is in only a small fraction of the population. Redevelopment of the ovary takes place, in part, almost as soon as the major brood is released and it is quite evident that small broods are produced later in the year, for a small proportion of specimens were found with eyed nauplii as late as August and September.

Table 2 gives notes supplied by Dr. Quayle on the appearance of the shore settlement of *B. glandula* based on observations made during the course of his own work. These, taken in conjunction with the estimated dates of release given above indicate a planktonic life of about 1 month; they also confirm that the major settlement takes place in the spring with some sporadic liberation into the early summer. His records of the presence of nauplii in the plankton on August 27 as well as September 20 in 1951 also confirm the production of a small autumn brood.

These results also accord with the observations of Johnson (1932) at Friday Harbor, somewhat to the south of Ladysmith; he

found barnacle larvae (species not stated) to first appear in the plankton in February with the maximum number in March and April. In a later paper with R. C. Miller (1935) he also refers to an autumn outburst of *B. glandula*.

The data in Table 3 indicate that at La Jolla the major portion of the sample was full of ripe unfertilised eggs by the end of September and early October. Fertilising began either in October or the early part of November and was complete by December; by the end of this month the greater proportion of the sample contained eyed nauplii, the large majority of which must have been released by the end of January. It is also evident that redevelopment of the ovaries takes place straight after shedding and that smaller broods are developed in March, April, and May inasmuch as up to 24 per cent of the individuals had eyed nauplii during this period. No breeding takes place after May, the ovaries gradually filling up to be ripe again by the end of September.

SIZE OF EGGS AND EGG PRODUCTION

The size of a number of egg cases with well-developed nauplii were measured. They

had a mean length of 0.22 mm. and a mean width of 0.125 mm. Fully developed eggs released from the ovarian tubules before they were fertilised had a diameter of 0.146 mm.

In order to measure the productivity the number of embryos in the egg masses of ripe

individuals was counted. Figure 2 shows a plot of the number of nauplii against the cube of the length of the adult. There is a linear relation suggesting, as might be expected, that the production is a function of the volume as has been found for other species (Barnes, 1953; Barnes and Barnes, 1954). The slope of the line is different, however, from that for the other species. Apart from any intrinsic differences in productivity the relation between volume and length cubed will vary from species to species.

DISCUSSION

Temperature data (means for several years) for La Jolla (kindly supplied by the Scripps Institution) and for protected areas in the neighbourhood of Ladysmith (see Hollister, 1954) together with values at Ladysmith for 1954, are given in Table 4.

At La Jolla the major brood of nauplii is fertilised in November, with a mean sea temperature of 16°–17°C., being released in January when the temperature (14°C.) is close to the minimum for the year. Smaller broods are produced up to May but none during the summer and autumn. Breeding only takes place when the temperature is below about

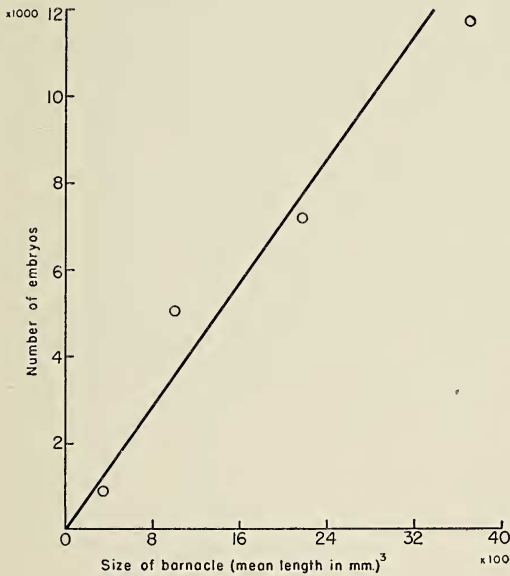


FIG. 2. Relation between number of embryos in the egg masses of ripe *B. glandula* and volume (cube of the length) of the adult.

TABLE 2
OBSERVATIONS ON THE SETTLEMENT OF *Balanus glandula* AT LADYSMITH

YEAR	MAIN SETTLEMENT AT LADYSMITH	REMARKS
1949	April 1	Sooke—May 16; lighter settlement at Ladysmith in July
1950	April 19	Intermittent settling until May 20; plankton still contained some nauplii and cyprids on May 22
1951		Nauplii in plankton from mid February to mid April; at intervals, May 9–21, July 31, August 27, September 20, none later
1952	About March 21	Week later at Ucluelet on west coast of Vancouver Island
1953	April 15	Light settlement at Comox (100 miles north of Ladysmith) on April 14
1954	April 1–6	Light settlement about June 1
1955	April 10, light, April 20, main set, lasting until end of April	At Crofton (8 miles south of Ladysmith) set during first week of May

TABLE 3
CONDITION OF THE OVARIES OF SPECIMENS OF *Balanus glandula* TAKEN AT LA JOLLA THROUGHOUT THE YEAR

DATE	PERCENTAGE OF SPECIMENS			
	Eggs unfertilised, not well defined	Eggs unfertilised, well defined, creamy yellow	Eggs fertilised, yellow	Eyed nauplii present yellowish brown to brown
20/ 7/54.....	24	76		
23/ 8/54.....	8	92		
23/ 9/54.....	15	85		
22/11/54.....		61	24	15
29/12/54.....			17	83
31/ 1/55.....		45	45	10
3/ 3/55.....		40	36	24
20/ 5/55.....		79		21
25/ 6/55.....	33	67		

TABLE 4
TEMPERATURE DATA FOR LA JOLLA AND LADYSMITH

	LA JOLLA (mean of 27 years)	LADYSMITH REGION 1952	LADYSMITH, 3 FEET BELOW SURFACE AND 50 YARDS FROM SAMPLING POSITION, 1954
January.....	14.0	6.2	4.7
February.....	13.9	6.1	5.9
March.....	14.5	6.7	7.0
April.....	15.5	8.2	8.7
May.....	17.2	10.9	13.0
June.....	18.6	13.1	14.7
July.....	19.8	15.4	18.2
August.....	20.6	15.1	18.1
September.....	19.2	13.4	14.5
October.....	18.0	12.1	11.4
November.....	16.3	8.8	9.2
December.....	15.1	7.7	7.1
Average.....	16.9	10.3	11.0
Maximum.....	20.6	15.4	18.2
Minimum.....	13.9	6.1	4.7
Range.....	6.7	9.3	13.5

17°C. At Ladysmith the major brood is fertilised and indeed released during the colder parts of the year when sea temperatures are between 6° and 8°C. However, there is an autumn brood, shed in August and September, which may have been fertilised in June and July when the temperature is again about 17°C. Bearing in mind the northward extension of the species the evidence suggests that the southern limit is determined by minimum temperatures of the order of 17°C., a lower temperature being required for breeding.

When the effects of competition with warm water species are taken into account this is in agreement with the fact that, as far as can be ascertained, temperatures at Ensenada, presumably taken offshore (U. S. Navy Hydrographic Office, 1944), are almost uniform throughout the year, never falling below a mean monthly value of about 15°C.

The upper temperature limit for breeding which takes place in the coldest months of the year is in agreement with a wide distribution northwards. However, if as suggested the

temperature barrier is at 16°–17°C., temperature conditions do not limit the breeding to the colder months of the year at Ladysmith and regions farther to the north; the breeding rhythm is tied to some other factors.

In *B. balanoides*, a boreo-arctic species, breeding appears to be determined by a temperature barrier at about 8°C. so that the southern limit is determined by the southern limit of the mean winter isotherm of 8°C. (Hutchins, 1947). It is found, therefore, farther south on the eastern seaboard of North America than on the coast of Europe as a result of the cold currents coming down the former coast. *B. glandula*, if a boreo-arctic species, seems to have raised the temperature barrier much higher so that it extends farther to the south on the western coast of America. It is of interest to note, however, the resemblance to *B. crenatus* which even near the southern limits of its distribution produces a second brood in the autumn of the year although it is considered to be an arctic species—more so than *B. balanoides*.

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